Respiratory development in a captive-born bottlenose dolphin *Tursiops truncatus* calf

V.M. Peddemors*
Biology Department, University of Natal, King George V Avenue, Durban, 4001 Republic of South Africa

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Changes in calf–mother association are examined and correlated to respiratory changes. This calf–mother respiratory association disappears within the first year. Data indicate that the first 6 h post partum are the most critical in gaining respiratory efficiency. Although respiratory data were only collected during periods of rest, changes in respiration rate appear to be strongly associated with the metabolic state of the calf. Stress loads of various forms affect the maximum breathhold ability more than the mean respiration rate. The mean length of apneustic plateau increased from 24 s to 40 s during the 18 month study period.

Variasies in kalf–moeder verhouding word ondersoek en met asemhalingsvariasies gekorreleer. Hierdie kalf–moeder asemhalingsverhouding blyk binne die eerste jaar te verdwyn. Data dui aan dat die eerste 6 h na geboorte die mees kritieke is om asemhalingsdoeltreffendheid te bereik. Alhoewel asemhalingsdata slegs gedurende tye van rus ingesamel is, blyk dit dat variasies in asemhalingstempo sterk met die metaboliese toestand van die kalf korreleer. Verskillende vorms van beklemming affekteer die maksimum-aseminhouvermoë meer as die gemiddelde asemhalingstempo. Die gemiddelde aseminhouvermoëvlak het van 24 s tot 40 s gedurende die 18 maande-studietydperk gestyg.

* Present address: Natal Sharks Board, Private Bag 2, Umhlanga Rocks, 4320 Republic of South Africa

The respiratory rhythm in the dolphin is unusual in that there is an extended pause — an apneustic plateau — between periods of inspiration and expiration. This rhythm has been observed under waking conditions, during sleep and also when the animal is anesthetized. Dolphins, on average, hold an apneustic plateau for between 20 and 50 s (McCormick 1969). Although Lilly (1966) suggested that respiration in dolphins is voluntary, McCormick (1969) indicated that it can be either automatic or can be brought under voluntary control, just as in other mammals.

O_2–CO_2 respiratory control in bottlenose dolphins *Tursiops truncatus* is similar to that of other mammals, except that tolerance to CO_2 in the blood is greater owing to increased buffering capacity (McCormick 1969). Ridgway, Scronce & Kanwisher (1969) calculated that the expired breath in these dolphins may contain as little as 1,5% O_2 after prolonged breath holding. The vital capacity of bottlenose dolphins is as much as 90% of the total lung volume (Irving, Scholander & Grinnel 1941). Upon scaling comparisons, the 26 l vital capacity for *Tursiops gilli* is about 0,91 $l.kg^{-1}$ body weight, and, based on body weight, the peak expiratory flow rate is 0,57 $l.s.kg^{-1}$ (Kooyman & Cornell 1981). A rapid tidal exchange is needed so that little delay occurs at the surface as the animal rolls through the air/water interface. Both *Tursiops* (Kooyman & Cornell 1981) and *Phocoena* (Kooyman & Sinnet 1982) have been shown to have an expiration time of 0,3 s.

Although the physiology of respiration in the bottlenose dolphin has been well investigated, the postnatal development of this specialized respiratory type is poorly documented. McBride & Kritzler (1951), Gurevich (1977) and Cockcroft & Ross (1990) found a decrease in respiration frequency with calf age, however only Cockcroft & Ross (*op. cit.*) link this to changes in the mother–calf bond.

In this study the development of neonatal *Tursiops* breath-hold capability and the role that mother–calf association plays in the determination of respirational ability, are investigated. The use of respiration rate as a tool to determine the stress levels of captive dolphins is also investigated, as there is an extremely high death rate of captive-born dolphin calves within the first year post partum (Ridgway & Benirschke 1977).

Methods

This study included three bottlenose dolphin calves, a *Tursiops truncatus, T. aduncus* and 'hybrid' *T. truncatus* × *T. aduncus* calf, all born at the Durban Sea World.

The main study animal was the *Tursiops truncatus* calf for which respiratory data were collected during 114 sessions, totalling 1152 h of observation over 18 months (Table 1). Observations were held at regular intervals throughout the study, with a minimum of one continuous 24-h watch completed per month. Respiration rates were collected at random intervals throughout the day for a minimum sampling time of 10 min. These samples were only started once the animal was well established in any particular behaviour, i.e. the behaviour was in progress for more than 2 min before sampling. It was intended that any effects on the metabolic state of the animal through the previous behaviour would be minimized. The apneustic plateau (a.p.) was recorded in seconds each time the animals surfaced to breathe. The respiration frequencies of both the mother and calf were recorded to indicate any breakdown of synchronicity in breathing. Time of day and associated behaviour patterns were recorded.

Respiratory data for the Indian Ocean bottlenose dolphin (*Tursiops aduncus*) and hybrid calves were

Table 1 Distribution of observation time during the study period

Month	Hours of observation
1	465 : 30
2	70 : 00
3	66 : 20
4	41 : 50
5	34 : 35
6	38 : 50
7	38 : 00
8	21 : 50
9	23 : 40
10	28 : 20
11	12 : 15
12	32 : 40
13	26 : 35
14	15 : 15
15	60 : 30
16	44 : 15
17	53 : 30
18	40 : 00
19	37 : 30
20	8 : 30
Total	1151 : 55

collected in a similar manner. For the *T. aduncus* calf, which died after 96 h, data were collected during regular (hourly) 10 min sampling periods throughout its life. In contrast, respiratory data for the hybrid calf were collected for the first 10 days post partum.

Only respiratory data recorded during sleeping or rest periods were included in analyses as the amount of exertion during other behaviours varied considerably, this variablity probably increasing with age.

For analysis, respiration data were categorized into two sets: (i) Calf breathing alone; (ii) calf breathing with mother. Three mean apneustic plateaux were calculated:
(a) Hourly mean = the mean of all recorded apneustic plateaux for the 10-min sample within that particular hour;
(b) Daily mean a.p. = the mean for all apneustic plateaux recorded during that day;
(c) Mean of the three longest apneustic plateaux for all records of the day.

Results

Initial post partum respiratory behaviour was characterized by the calf leaping so that the entire torso left the water surface at approximately 45° (Figure 1). By the 25th day post partum the calves had all acquired the smooth roll which characterizes the respiratory surfacing of the adult.

Initially the mean a.p. for all calves was 13 s, however this increased rapidly within the first 12 h (Figure 2). The breathing rate of both the *T. truncatus* and hybrid calves remained fairly constant after the first day, the a.p. fluctuating within the same range for both calves (Figure 2). It was during the first 24 h that the interaction between mother and calf changed most dramatically. The daily minimum and maximum apneustic plateaux were constant for both calves throughout the first 10 days post partum (Figure 2), even though the mother–calf association decreased to such an extent that by the 10th day the calves were consistently swimming approximately 50 cm from their mothers' flanks, rather than being tucked into the echelon position.

Figure 1 Calf leaping clear of water during initial post partum synchronous respiratory behaviour.

The *T. aduncus* calf was the only animal to show an increase in respiratory rate (Figure 2), which may be attributed to ill health prior to death.

For the *T. truncatus* calf the greatest mean breathhold of 51 s was reached by the 14th day (Figure 3). During the first two weeks post partum the *Tursiops truncatus* calf exhibited an increasing ability to hold its breath for long periods, as indicated by both the mean and longest apneustic plateaux (Figure 3). Thereafter the mean a.p. decreased to a range maintained for the following five months (Figure 3). A dramatic increase in maximum breath-hold ability occurred around six months post partum, a phenomenon not as pronounced in the daily mean a.p. (Figure 3). This change appeared to be directly related to mother–calf association during respiration, as both Figure 4 and Figure 5 indicate a breakdown of this association during this period.

Although all respiration counts were made during what was defined as resting behaviour, it was still highly variable (Figure 3). There was a significant difference between the graph mean and periods of increased respiration (Student's t test; $p > 0{,}05$). This variability corresponded to periods when the animals were subjected to stress loads of some form, e.g. new environment (days 28–46), ill health (day 537), excessive handling (day 550).

There appear to be three phases within mother–calf association (Figure 4). During the first 50 days more than 90% of the calf's respirations were taken in synchrony with its mother (Figure 4). Subsequently, synchronous respirations decreased rapidly to around 20% of all breaths (Figure 4). This change corresponded with a behavioural change during sleep. The calf would rub

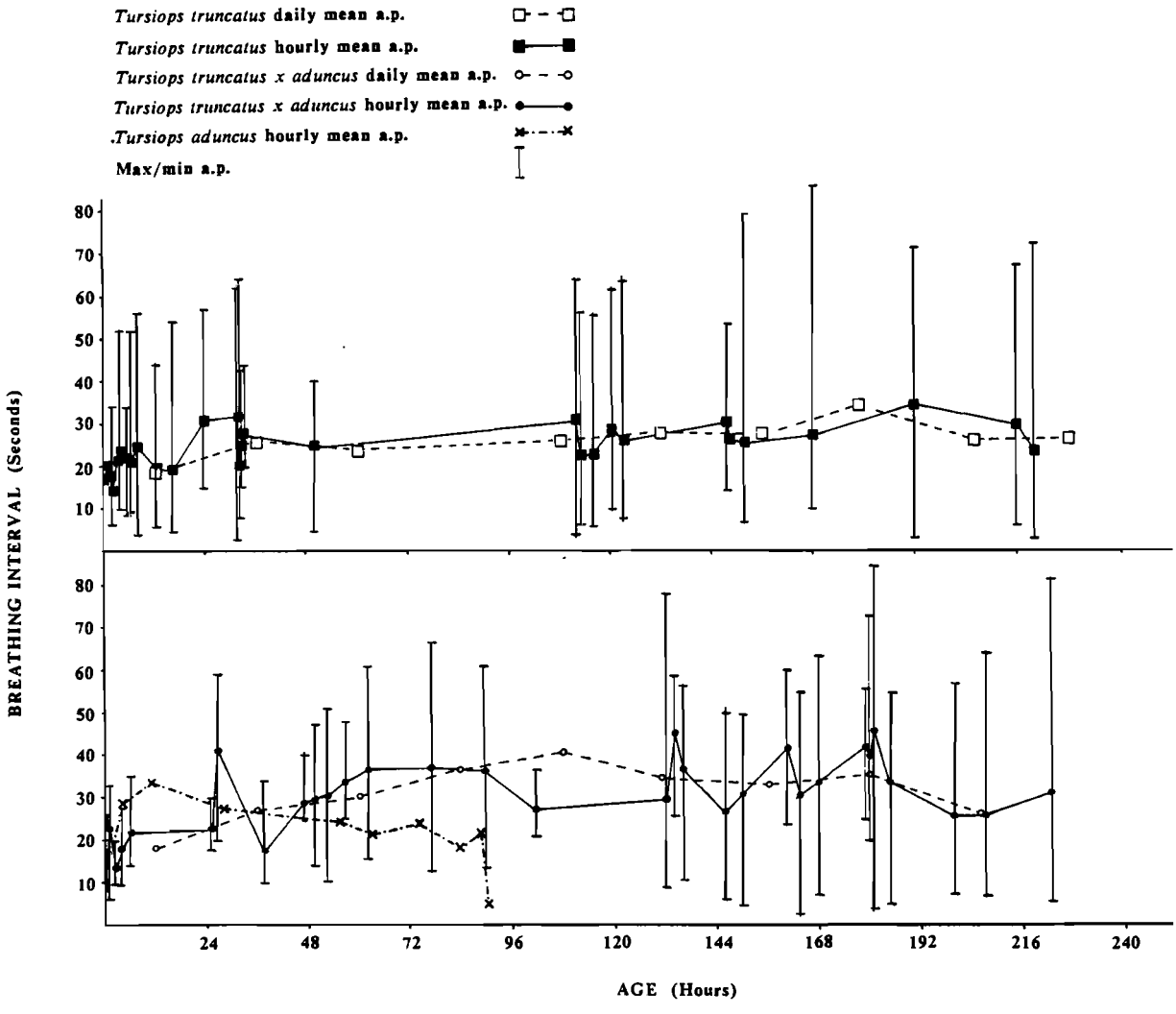

Figure 2 Changes in respiratory interval for the *Tursiops* calves during the first 10 days post partum.

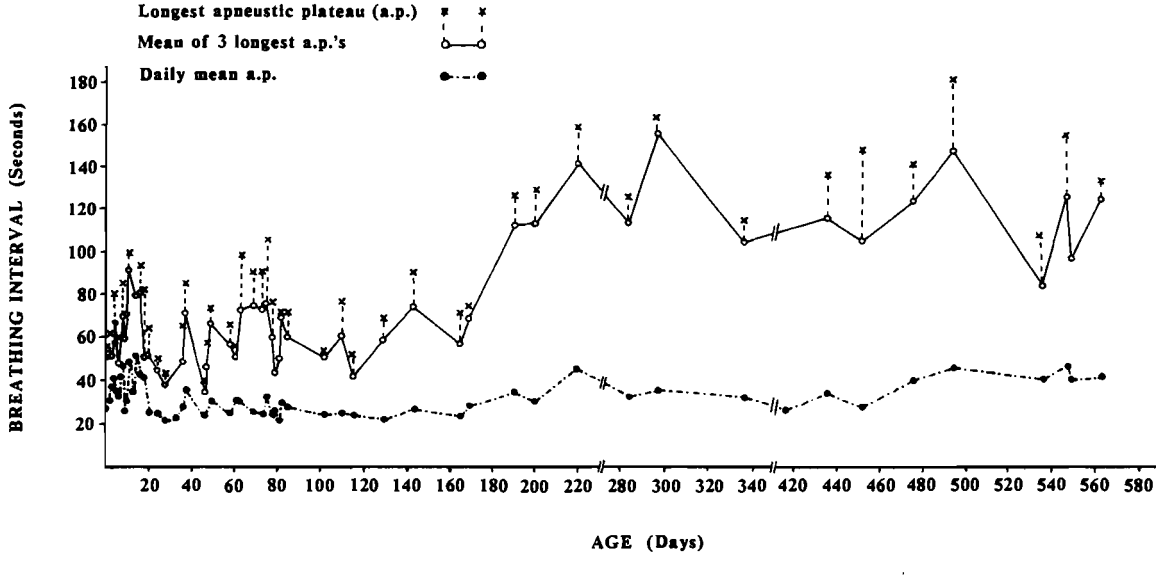

Figure 3 Changes in mean and maximum apneustic plateau for *Tursiops truncatus* during the study period.

past alternate flanks of his mother whilst she was lying on the bottom, only respiring at the end of every side's rub past. Whilst this type of sleep behaviour persisted (approximately 70 days), the associated respiration pattern remained constant (Figure 4). A final break-down in respiratory association occurred after six

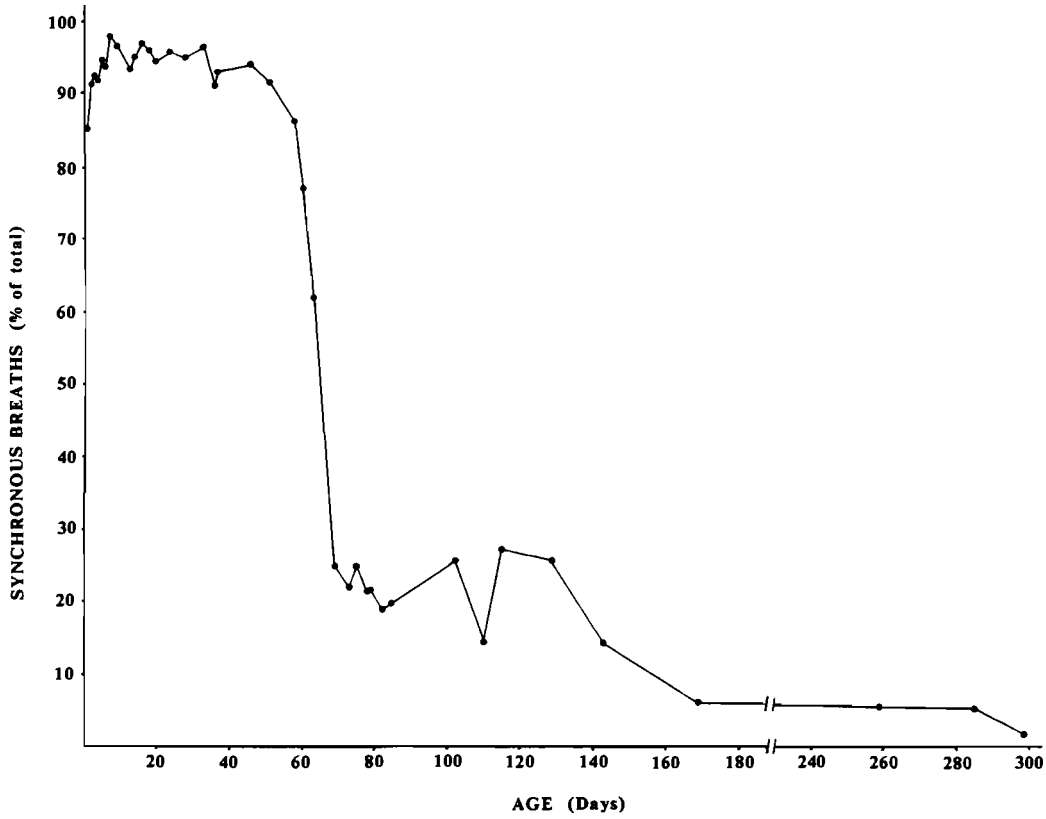

Figure 4 Percentage of the *Tursiops truncatus* calf's respirations in synchrony with its mother.

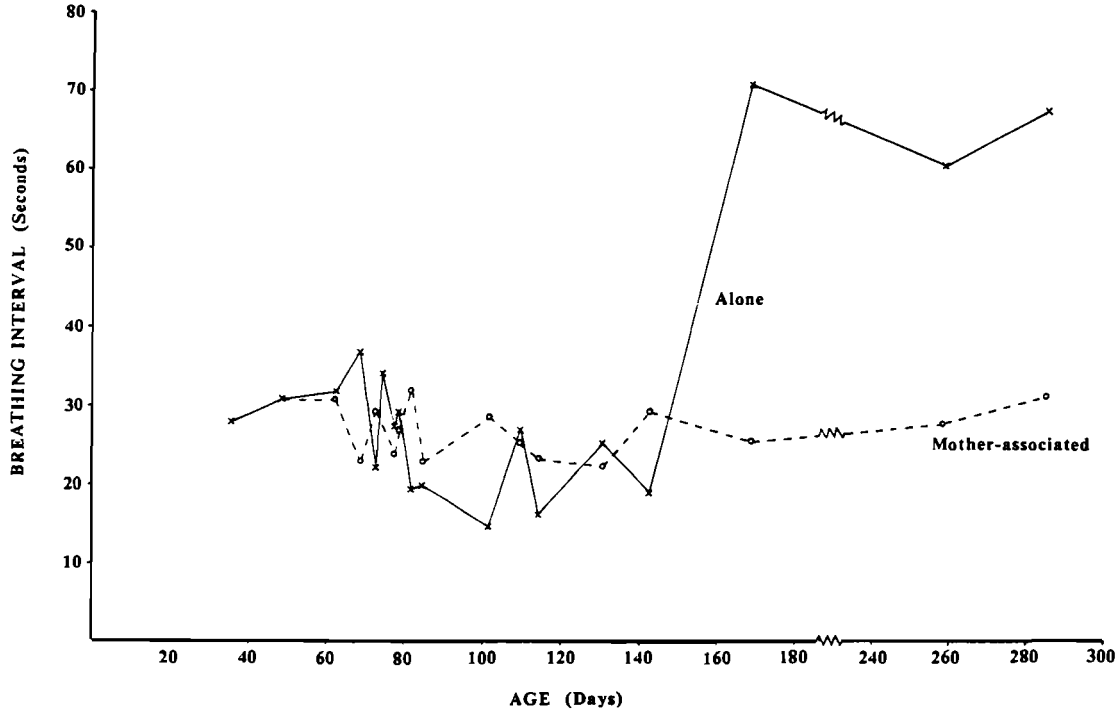

Figure 5 Age-related changes in the mean respiratory interval for a *Tursiops truncatus* calf during respiratory associations with its mother.

months when less than 10% of mother and calf breaths were taken in sychrony (Figure 4). This coincided with the calf utilizing the newly aquired stationing behaviours of floating and/or lying on the pool bottom whilst asleep.

By 49 days post partum, the calf had initiated his own breathing pattern, which for the first 30 days held a longer a.p. than when respiring with his mother (Figure 5). Thereafter the calf respired less frequently with his mother (Figure 4) and changed to have a shorter a.p. when breathing alone (Figure 5). At six months post

partum this changed to an average of 40 s longer than when taken in association with the mother, a phenomenon persisting to the end of the study (Figure 5).

Discussion

Why neonatal dolphins respire by raising their entire heads above the water surface is unclear. It may increase the period that the blowhole is exposed, allowing more time for tidal exchange. Alternatively, it may simply be a function of aquiring motor control. The change to the normal rolling action at the water/air interface could, therefore, be indicative of the calf's development.

During the first few hours post partum the female and calf are probably under maximum predatory exposure, the scent of blood and afterbirth filling the surrounding waters. At this time the mother's swimming ability is hampered by the respiratory inefficiency of her calf, and possibly by the unexpelled placenta, which may take between 2 and 16 h to eject (Peddemors, unpublished data).

Immediately after birth dolphin calves are collected by the mother and are kept in a protected position at the mother's side by slipstreaming (McBride & Kritzler 1951; Essapian 1953; Norris & Prescott 1961; Peddemors 1987; Cockcroft & Ross 1990). For the first 2 h the calves tended to ride high up on the mother's flank adjacent to the dorsal fin, thereby enabling the mother to control the calf while it gained some motor coordination (Peddemors, *op. cit.*). During this initial period the calf breathes on its own while swimming near the surface, but, upon changing position to swim in the low pressure area at the mothers' side (the echelon position — Norris & Prescott, 1961) its respiration rate is governed by the mother.

The development of a prolonged a.p. is critical for dolphins, as almost their entire behavioural repertoire is performed underwater. As such, a.p. development is closely interlinked with behavioural development. As the calf ages it develops locomotor control and respiratory efficiency. A more efficient tidal exchange, in conjunction with efficient locomotor muscle use may require the calf to respire less frequently, thereby lengthening the a.p. This probably allows the calf's behavioural repertoire to rapidly expand and to complete complex behavioural patterns e.g. synchronous feeding.

The first 6 h post partum appear to be critical in gaining respiratory efficiency, as during this period the calf increases its a.p. ability most rapidly. This increase in the calf's respiratory rate during initial independent swimming is concurrent with a change in protective attitude, the calf now following the mother rather than the reverse (Peddemors 1987).

The phenomenon of rapid aquisition of a long a.p. may have a functional nature as the calf needs to be able to stay with its mother at all times to benefit from her protection. The mother therefore may have been enforcing long breathholds in succession to ensure that the calf is able to withstand such physiological stress if the need were to arise. In addition this, a.p. development is important to enable initiation of suckling behaviour.

After an initial rapid increase in respiratory efficiency, the a.p. increases steadily as the calf appears to learn to use its locomotor muscles and senses well enough to start leaving its mother's side. A similar period before the gaining of independence was noted for *Tursiops* by Tavolga & Essapian (1957), Tavolga (1966) and Gurevich (1977). It therefore appears that after birth there is a two week learning period during which the mother–calf association is strongest and the calf's respiratory rate is directly controlled by the mother. The large increase in breathing rate during the following week may be explained by changes in sleep behaviour. The swim pattern started including variations, such as figures of eight, instead of constant perimeter circling, and the calf started gaining some locomotory independence (Peddemors 1987). In addition, the initial close association between mother and calf had broken down to such an extent that by the 21st day no protective behaviour was exhibited by the mother when in the presence of divers. The calf had now apparently gained its swimming independence.

A number of studies suggest that weaning takes place at around six months (Prescott, 1977; Ridgway & Benirschke 1977; Cockcroft & Ross 1990; Peddemors 1987). The sudden rapid increase in maximum breathhold ability at this time suggests that there is a natural progression toward weaning, as a calf would require an extended a.p. to enable it to hunt for itself. Therefore, although the present analysis only included rest-associated apneustic plateaux, there may be a general increase in a.p. at this time of calf development.

Although the close association between mother and calf apparently ceases soon after birth, calves may continue to breathe in synchrony with their mother during sleep or rest periods for the first two months. During this period the mother still appears to have a strong influence over the calf as a calf will synchronize it's breathing to her breath rate.

Although it was hoped that the use of respiratory data recorded during resting behaviour would present as constant a metabolic rate as possible, the variations in behaviour exhibited during resting still appeared to bias the data. The variance in respiratory rate may reflect the metabolic state of the calf, either in extent of exertion, or in stress level.

The bodily changes which are likely to occur in conflict situations may be lumped under the term strain because the body's response to a wide range of 'stressors' is very similar (Manning 1979). Activity in the autonomic nervous system is increased, which upon stimulation of the adrenal medulla causes release of adrenalin into the bloodstream. This results in changes in numerous parts of the body, including more rapid and deeper breathing (Manning 1979).

The sudden rapid increase in respiration rate of the *T. aduncus* calf which occurred 4 h prior to death, possibly indicated the severe stress the animal experienced before succumbing to a suspected hepatic coma (Thurman & Williams 1986). Two hours prior to death the respiration rate had increased to an average of 12 breaths per minute. This rate is in the region of the maximum

breathing rate at any time for the other animals. Observations on the *T. truncatus* calf indicated that increases in respiratory rates could be related to the animals well-being. Similarly, Hester (1981) noted that increases in respiratory rate may result directly from disease or as a response to environmental changes. This suggests that stress factors have a greater effect on the maximum breath-hold ability than on the mean respiration rate. Stress can affect animals to the extent of causing death (Caldwell, Caldwell & Siebenaler 1965) so this phenomenon should be of obvious husbandry interest in monitoring the physiological and/or psychological state of captive animals. Normal respiration rates for each animal must, however, be known before such data is of any value.

Tracking of free-ranging marine mammals is possible owing to their requirement of regular surfacing to breathe. Although the entire school may surface at regular short intervals, no detectable stable relationship has been found in animals other than cow–calf pairs surfacing together (Wursig 1978; Rigley, Vandyke, Cram & Rigley 1981; Cockcroft & Ross 1990). Wursig (1978) found this mother–calf association still to be strong after two and a half years in one free-ranging pair; however, both the present results and those of Cockcroft & Ross (*op. cit.*) indicate this bond to be almost completely broken after one year for captive animals. This reduction in association period may be a direct consequence of the environment, as there is less need for protection and associated inter-relationship in captivity than in the natural habitat. The mother–calf bond therefore appears to exist for at least the first year post partum. The long period of respiratory control by the mother may be a reflection of the K-selection strategy of parental investment that dolphins employ. In addition this strong mother–calf bond may serve as an initiation to the hierarchical social structure existent in dolphin schools, where social bonds between animals may serve important roles in the altruistic behaviour often exhibited between animals (Connor & Norris 1982). This bonding may also assist researchers of free-ranging groups in determining the social structure and individual reproductive potential within such groups.

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